RESULTS AND DISCUSSION

Zooplankton

Annual Abundance and Biomass of Zoonlankton Groups

From 1986 to 1992, 65 species representing 38 genera from the Calanoida, Cladocera, Cyclopoida, Mysidacea, and Rotifera comprised the offshore zooplankton community of Lake Ontario (Table 14). Twenty-two common species plus their juvenile stages accounted for 97.6% of the total abundance and 96.0% of the total biomass (Table 15). Yearly data on common species are presented in Tables A 1 O-A l7 in the Appendix. The Rotifera contained the largest number of species (37, Table 14) and accounted for the highest relative abundance (64.2%). The Calanoida, Cyclopoida and the nauplius stage of the copepod represented 26.4% of the total zooplankton abundance during the 1986- 1992 period. The Cladocera (40.0%) followed by the Cyclopoida (32.3%) contributed the most biomass to the zooplankton community, while the Rotifera and the Calanoida represented 7.2% and 4.2%, respectively, of the zooplankton biomass (Table 14). These results are similar to distributions observed in 1967 (Patalas 1969): Cyclopoida-57.4%, Cladocera- 39.4%, Calanoida -3.2%. However, they differ considerably from the work of Mazumder et al. (1992) who observed rotifers to represent over 75% of the total zooplankton biomass in 1982. Within the 1986-91 period of this study, composition of the zooplankton community at the Order level or above has varied. Relative biomass of the rotifers decreased steadily, while cladoceran relative biomass declined sharply in 1990 to 11.1% and than rebounded to 63.3% in 1991 (Fig. 9) Average density and biomass for 1986-1992 (spring and summer) was 235.7 organisms/L ± 20.2 (mean ± S.E.) and 90.2 μg/L ± 9.2 (mean ± S.E.), respectively (Table 16). Biomass was higher in the summer (I 64 μg/L ± 13.9) than the spring (9.8 μg/L ± 0.7) (Tables 17 and IS).

Geographical Distribution of Zooplankton Groups

Trends in horizontal distribution of zooplankton biomass were not observed in each year or season. In the spring there was a tendency for zooplankton biomass to be higher at the eastern end of the lake (Fig. 10). This was particularly true in 1988, 1990 and 1991. Yet in 1992 spring biomass was higher at the western end of the lake (Fig. 10). During the summer little change in zooplankton biomass was observed from west to east with the exception of the summer of 1991 when zooplankton biomass was exceptionally high in the western portion of the lake (Fig. 10). The cause of the higher biomass from west to east in summer of 199 I was due to an increase in the abundance of *Daphnia retrocurva* and *D. galeata mendotae* in the western portion of the lake (Fig. 1 1). Others have observed horizontal differences in distribution that appear to be related to the seasonal thermal cycle (Patalas 1969). For example, in June and July of 1967, zooplankton were more abundant in the eastern end of the lake northeast of Sodus Bay, which is roughly equivalent to Stations 60 and 63 in this study. This distribution was less pronounced in August and September.

Historic Trends in Abundance

Results of zooplankton tows prior to 1986 were with unmetered tow nets. Taylor *et al.* (1 987) demonstrated that an unmetered sample net in Lake Ontario severely underestimated biomass during spring, early summer and fall, when colonial diatoms are abundant and net efficiencies are reduced. This was not the case in August. Thus there is some basis for confidence for comparison of the 1986-91 metered samples with the previously unmetered samples.

A comparison of the August Crustacea biomass of 1970, 1972, 198 l, 1982 and 1986-91 suggests there was an increase in zooplankton abundance from 1970 to 1972, but from 1972 to

199 I, crustacean abundance remained nearly steady (Fig. 12a). The minimum in zooplankton abundance occurred during the summer of 1987 when Bvthotrephes cederstroemi was reported in some portions of Lake Ontario, but not in our samples.

An interesting increase in spring zooplankton abundance started in 1986 (Fig. 12b). Abundance increases in juvenile and adult calanoids (Diantomus minutus, D. oregonensis, D. sicilis, Limnocalanus macrurus) and cyclopoid copepoditcs and Cyclops bicuspidatus thomasi appear to be the probable cause (Table 19).

Historical Changes in Species Comnosition

Roti fera

Nauwerck (1978) studied the composition, abundance, and morphometrical properties of rotifers in Lake Ontario in 1970. Average abundance in April 1970 was 10,500/m^3 with Svnchaeta (83% of total abundance) being the overwhelming dominant. In August of 1970, species of Polvarthra accounted for 45% of the abundance followed by species of Keratella. Maximum rotifer abundance occurred in July (220,000/m^3) of 1970 followed by a sharp decline in August to less than 58,400 individuals/m^3. In 1982, Mazumder et al. (1992) observed that rotifer abundance was significantly higher than in 1970, and that species of Polvarthra and Keratella were dominant with Synchaeta sp. contributing only 6% of the spring abundance and Conochilus and Trichocerca contributing as much as 80% of the total spring abundance. In the 1986 to 199 l period, average rotifer abundance in April (6,500/m^3) and August (64,700/m^3) were similar to those in 1970 (April =10,500/m^3; August= 58,400/m^3).

In August of the 1986- I99 l period, the dominant (numerically) rotifers in Lake Ontario were two species of Polvarthra (P. vulgaris and P. major) and two species of Keratella (K. crassa and K. cochlearis) that accounted for 45.6% of the total zooplankton abundance and 5.6%

of the total biomass (Appendix A10-A17). As in April of 1970, Synchaeta sp. was the numerically co-dominant rotifer in April of the study period (mean = 15.9% of the total abundance) along with Notholca squamula (12.9%) and Kellicottia longispina (9.3%). Prominent spring and summer rotifer species from 1986 to 1992, in descending rank as abundance, were: Polvarthra vulgaris, Keratella cochlearis, K. crassa, P. major and Kellicottia longispina (Table 15). Of the dominant rotifers, Polvarthra vulgaris, Polvarthra major, and Keratella cochlearis are cosmopolitan, curytopic species. The eutrophic indicators Filinia longiseta ($334/m^3$), Trichocera cvlindrica (mean=$53/m^3$) and Trichocerca multicrinis (mean=$2,630/m^3$) were present in Lake Ontario but had relatively low abundance (i.e. accounted for less than 1 .O% of the biomass and abundance). The lack of dominance of eutrophic indicator species for the entire lake suggests that the offshore waters of Lake Ontario during the 1986-92 study period were not eutrophic. This would agree with the conclusion derived from phytoplankton indicator species and the algal biomass classification of trophic status (This study). Taylor et al. (1987) reached a similar conclusion based on total phosphorus and chlorophyll concentrations.

Crustacea

Prior to the 1970s, there were few studies of the zooplankton of Lake Ontario and, in most cases, these were of the nearshore region or attached bays (Marsh 1901, Whipple 191 3, Hart 1930, Pritchard 193 l, Tressler and Austin 1940, Tressler et al. 1953, Brooks 1957, Anderson and Clayton 1959, Robertson 1966, McNaught and Fenlon 1972, Wilson and Rolf 1973, Czaika 1974). Crustacean studies of the offshore waters of the Lake Ontario basin are fewer in number. Patalas (1969) collected monthly vertical hauls (64 pm net) from 0 to 50m, lakewide, from June to October 1967, while Watson and Carpenter (1974) sampled 33 stations lakewide in 1970 with a 64-μm mesh net. In 1972-73, the most extensive lakewide studies (60 stations, 64-μm net) were undertaken during IFYGL (International Field Year for the Great Lakes, McNaught 1975). More recently, Johannsson et al. (1985a, 1991) sampled at four stations (two nearshore, two offshore) in 198 1 and 1982 with a 64 or 70-μm mesh net (0-20m sampling depth) and Taylor et al. (1987) sampled at three stations with a 64-μm mesh net in 1982. August data have been extracted from the previous data sets to allow comparison with the 1986- 199 1 data sets.

In 1967, Cyclops bicusnidatus thomasi and Tronocvclons prasinus were the most abundant cyclopoids, while Bosmina longirostris and Daphnia retrocurva were the most abundant cladocerans (Patalas 1969). These same four species were predominant in 1970 (Watson and Carpenter 1974), 198 1-82 (Johannsson et al. 1985a and b) and 1986- 199 1 (this study). From 1970 to 1991, Ceriodanhnia lacustris and Eubosmina coregoni were always present but not predominant. Calanoid copepods have not been abundant since at least the late 1960's. However, the calanoids Eurytemora affinis, Diaptomus sicilis, D. oregonensis, D. minutus and Limnocalanus macrurus were caught in all studies, including this one. Calanoids are believed to have been the dominant group in Lake Ontario at one time (Robertson and Scavia 1984), with the shift from a calanoid dominated to a cyclopoid/cladoceran community occurring from 1939 to 1973 (McNaught and Buzzard 1973) .

However, there are changes in the August composition and abundance of the zooplankton during the period from 198 I-82 to 1986-9 1. Ceriodanhnia lacustris decreased in abundance from 198 1 (2,962/m^3) to 1988 (3 14/m') and was not observed after 1988 (Table 20). Abundance of Bosmina longirostris decreased from the 80,000 to 140,000/m^3 range in 198 l-82 to less than 7,500/m^3 in 1991 (Table 20). Abundance of Dauhnia retrocurva in 1991

($36,187/m^3$), however, was its highest in over 20 years. After 1986, the larger Daphnia galeata mendotae was more prevalent than in the early 1980s and early 1970s with abundance being substantially higher in 1987 (9,200/ m") and I99 1 ($3,500/m^3$). Abundance of the cyclopoid Cyclops vernalis was also substantially higher in 1987 and 199 l than at other times over the last 24 years, while Cyclopoida copepodites have averaged around $40,000/m^3$ since 1988 compared to $25,000/m^3$ prior to 1987. Similarly, the larger bodied Polyphemus pediculus, Holopedium gibberum and Leptodora kindtii appear to be more prevalent in the 1986-1991 period than in 1972 and 198 l/82 (Table 20). Abundance of Diaptomus oregonensis, D. minutus, D. sicilis, Eurvtemora affinis, the immature stages of the calanoid, and the oligotrophic indicator species Limnocalanus macrurus have increased substantially since 1972 and 198 l/82 (Table 20). Abundance of the nauplius stage of the copepod was especially higher in the spring during the study period compared to the early 1980s (Table 20). Calanoida composition and abundance in the summer of 1990 and 199 1 were more similar to that of 1970 than those of 1980- 198 1.

The large predaceous cladoceran Bvthotrephes cederstroemi was first observed in nearshore waters of Lake Ontario in 1985 (Lange and Cap 1986). Although observed only rarely in our spring and August sampling of the offshore waters of Lake Ontario during the 1986-9 1 period (Table 20), Bythotrenhes cederstroemi was relatively abundant in the autumn of 1987 (102/m’) (This study). A similar autumn abundance was observed by Johannsson et al. (1991) at another site in Lake Ontario in 1987. In the spring and summer of 1988, B. cederstroemi was not observed in net samples but was found in the guts of alewife (Mills et al. 1992). Abundance in August of 1990 was low (4 individuals $/m^3$) and they were not observed in 1991.

In general, abundance of smaller species has decreased and larger cladoceran, calanoid and cyclopoid species have become more prevalent within the pelagic region of Lake Ontario from 1970 to 1991. Average length of the cladoceran community increased over the period of this study (Fig. 13) and it was negatively correlated with alewife abundance (Fig. 14). In particular, species of Danhnia (D. retrocurva and D. galeata mendotae) and Bosmina longirostris have increased in size (Fig. 1.5) by an average of 66% from their minimum length in the 1986 to 1991 period. An apparent negative correlation between average calanoid and cyclopoid length and smelt abundance was not statistically significant (Fig. 14).

General Discussion

The offshore waters of Lake Ontario had two major vertebrate planktivores during the period of this study, the alewife Alosa pseudoharengus and the rainbow smelt Osmerus mordax (Johannsson and O'Gorman 1991) with the alewife being the most abundant fish in the lake (O'Gorman et al. 1987). During summer stratification the smelt are generally found beneath the epilimnion while alewives are confined largely to the epilimnion (Olson et al. 1988). The most important factor determining the zooplankton composition of Lake Ontario during the 1980s and early 1990s was probably the intense planktivory by alewifes (Taylor et al. 1987). Alewives spatially concentrate and are known to locally depress zooplankton body size and abundance in Lake Ontario (O'Gorman et al. 1991). Planktivore abundance in Lake Ontario has varied greatly over time. The late 1960's and the early 1970's were periods of high alewife abundance accompanied by nuisance die-offs. Much lower alewife biomass existed in the mid- 1970's possibly due to increased numbers of salmonine fishes but especially following a major episode of winter mortality in 1976 (Taylor et al. 1987). Results from assessment trawling in U.S. waters of Lake Ontario indicate increasing numbers of alewives from 1978 to 1982 (O'Gorman and Schneider 1986). Alewife and rainbow smelt biomass declined irregularly but steadily from 198 1 to 1990, and maintained uniformly low levels from 1990 to 1992 (Fig. 16).

Bythotrephes predation on zooplankton can be extensive and affect community species assemblage and abundance (Lehman 199 1, Lehman and Caceres 1993, Makarewicz et al. 1996). Its presence in Lake Ontario was brief, however, with maximum abundance limited to the fall of 1987. In fact, Bythotrephes was not observed in our samples in August of 1987, although Makarewicz and Jones (1990) observed it at a single site in 1987. Bythotrephes appeared to have minimal, if any, effect on zooplankton size and composition in August of 1987 or in 1990 when B. cederstroemi reappeared in the water column (mean = $4/m^3$). However, zooplankton abundance was lower in 1987 than in 1986 or 1988- 199 1 (Fig. 12). Abundance of B. cederstroemii in Lake Ontario in August of 1987 and 1990 was apparently below a minimum threshold level to significantly affect zooplankton populations.

O'Gorman et al. (1991) suggest that information on zooplankton size in large, cold-water lakes can be linked to changes in abundance, condition and growth of planktivorous species. For example, Langeland (1978) observed that the mean sizes of D. galeata mendotae and Holopedium gibberum decreased as predation pressure from Arctic char increased. In Lake Michigan, average zooplankton length increased dramatically as alewife abundance decreased (Makarewicz et al. 1995). Other indicators of increased planktivory in planktivore-dominated systems include shifts in Cladocera composition toward smaller species and a decrease in total zooplankton abundance as well as changes in productivity and the the number of eggs per individual (Johannsson et al. 199 1, Johannsson and O'Gorman 199 1).

In Lake Ontario, the resurgence of larger Calanoida and Cyclopoida in the spring and the increased length of Cladocera suggest a decrease in alewife planktivory. Over the past 10 years, relaxation of alewife predation in Lake Ontario is often cited as the partial cause of either appearance or the higher abundance of large zooplankton species, such as Bvthotrephes cederstroemi in 1987 and Mysis relicta in 1984 (Makarewicz and Jones 1990; Shea and Makarewicz 1989, Johanssson et al. 199 1). Certainly, the increase in summer abundance of the larger calanoids and the predaceous and herbivorous cladocerans and the increase in length of Daphnia spp. and Bosmina in the early 1990s suggest a scenario of decreasing alewife predation on zooplankton. The changes in zooplankton composition observed were not likely a result of relaxation of invertebrate predation. Abundance of Polyphemus pediculus and Leptodora kindtii increased in abundance rather than decreased. The decrease in abundance of the small cladocerans B. longirostris and C. lacustris during the 1989-199 1 period may be due to the increase in abundance of the D. retrocurva and the larger D. galeata mendotae that resulted from relaxation of size-selective predation by alewives on Daphnia. Vanni (1986) demonstrated that a large herbivorous zooplankton, such as Danhnia, can reduce the density of small zooplankton, such as Bosmina by competition for resources.

The changes in the zooplankton community observed do not refute Taylor's et al. (1987) prediction that as planktivory by fish declines, the role of herbivores in the spring and early summer plankton will pass from rotifers and ciliates to calanoid copepods. Such a major change in zooplankton composition has not taken place; although we may be observing the beginning of the process. Abundance of calanoid copepods has clearly increased. Our data demonstrate that the composition and abundance of the zooplankton community of Lake Ontario has changed in response to a relaxation of alewife predation.

Prior to 1990, the size composition of small species that dominated the zooplankton community suggests a community characteristic of planktivore-dominated systems where the fish feed selectively on larger individuals. After 1990, our data show that calanoids are more important in the pelagic of Lake Ontario than they have been in 20 years; that smaller cladocerans are decreasing in abundance while increasing in size; that *Danhnia* are more prevalent and increasing in size as an inverse function of alewife abundance; and that large predaceous cladoceran species are more prevalent than they have been prior to 1970. The zooplankton community of Lake Ontario has been responding to changes in the forage fish community ultimately caused by continued predation pressure of salmonines.